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Long-term indirect effects of mechanical cockle-dredging on intertidal bivalve stocks in the Wadden Sea

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Summary

1. There is world-wide concern about the effects of bottom-dredging on benthic communities in soft sediments. In autumn 1988, almost a third of the 50-km² intertidal system around the island of Griend in the western Dutch Wadden Sea was suction-dredged for edible cockles Cerastoderma edule and this study assessed subsequent effects. An adjacent area not directly touched by this fishery and an area from which the mussel Mytilus edulis beds were removed, served as reference areas.

2. Sediment characteristics, together with the total stock size and settlement densities of Cerastoderma, Baltic tellin Macoma balthica and soft-shelled clam Mya arenaria, were documented during 11 successive autumns before (August–September 1988) and after (August–September 1989–98) the suction-dredging event in fished and unfished areas. Four other areas in the Dutch Wadden Sea, where changes in densities of juvenile bivalves from 1992 to 1998 were measured, served as additional reference locations.

3. Between 1988 and 1994, median sediment grain size increased while silt was lost from sediments near Griend that were dredged for cockles. The initial sediment characteristics were re-attained by 1996.

4. After the removal of all Mytilus and most Cerastoderma, the abundance of Macoma declined for 8 years. From 1989 to 1998, stocks of Cerastoderma, Macoma and Mytilus did not recover to the 1988 levels, with the loss of Cerastoderma and Macoma being most pronounced in the area dredged for cockles. Declines of bivalve stocks were caused by particularly low rates of settlement in fished areas until 1996, i.e. 8 years after the dredging.

5. A comparison of settlement in the short (1992–94) and medium term (1996–98) after cockle-dredging in several fished and unfished areas spread over the entire Dutch Wadden Sea, showed a significant negative effect of dredging on subsequent settlement of Cerastoderma. Macoma also declined, but not significantly.

6. We conclude that suction-dredging of Cerastoderma had long-lasting negative effects on recruitment of bivalves, particularly the target species, in sandy parts of the Wadden Sea basin. Initially, sediment reworking by suction-dredging (especially during autumn storms) probably caused losses of fine silts. Negative feedback processes appeared to follow that prevented the accumulation of fine-grained sediments conducive to bivalve settlement.

Key-words: BACI, benthic communities, conservation, fishery, soft sediments, spatfall.

Introduction

There is widespread concern that many forms of bottom-fisheries damage the epi- and infrafaunal communities of intertidal and subtidal sediments (Dayton et al. 1995; Brown & Wilson 1997; Fogarty & Murawski 1998; Jennings & Kaiser 1998; Hall 1999; Kaiser et al. 2000). Bottom-fisheries not only remove the target species (Robinson & Richardson 1998) but also impact on associated flora and fauna (de Vlas 1987b; Bergman & Hulscher 1991; Brylinsky, Gibson & Gordon 1994; Beukema 1995; Ferns, Rostron & Siman 2000). In addition, trawling, dredging and digging usually remove benthic communities on the surface that are not easily replaced, such as mussel beds or banks of tube-living polychaetes, even when such elements are not the target of the fisheries (Reise 1982; Roberts 1997; Service & Magorrian 1997, Hall 1999). Depending on the scale of the fisheries and the local hydrological conditions, these effects on non-target organisms or structures, often responsible for key benthic processes, may also lead to changes in sediment characteristics (Shand 1987; Churchill 1989; Hall 1994; Smelgroeve & Butman 1994; Oost 1995; Newell, Seiderer & Hitchcock 1998). Recovery may be slow (Collie et al. 2000), with benthic communities substantially changed (Roberts 1997; Hall 1999).

Of the four common bivalves in the intertidal area of the Dutch Wadden Sea [blue mussel Mytilis edulis Linnaeus, edible cockle Cerastoderma edule (Linnaeus), Baltic tellin Macoma balthica (Linnaeus) and soft-shell clam Mya arenaria (Linnaeus)], the mussels and cockles are commercially exploited. These species overlap in their algal food and time of feeding (Kamermans 1994) and grow more slowly where conspecifics or other bivalves are at high density (Kristensen 1957; Jensen 1992). Given that suspension- and deposit-feeding bivalves can be regarded as food-competitors (Kamermans et al. 1992; Beukema & Cadée 1997), the commercial removal of the stocks of one or two of these species could relax competition for food. This might result in enhanced fecundity and greater stocks of the non-target species.

We compared changes in sediment characteristics and abundance of three bivalve species at different intertidal sites in the Dutch Wadden Sea. Most of the data were collected during a long-term study to determine the year-to-year variations in food supply at a stopover and a wintering area of a long-distance migrating shorebird, the red knot Calidris canutus (Linnaeus) (Piersma et al. 1993, 1995). Over 11 consecutive seasons, in late July–September 1988–98, the distribution and abundance of molluscs on the intertidal areas around Griend were mapped in relation to sediment characteristics. Early in the study, in late September 1988, the large stocks of cockles in the northern part of the study area were mechanically harvested. Over the subsequent two winter seasons, two complexes of mussel beds in the western parts were also removed for commercial reasons. By analysing changes in sediment characteristics and bivalve stocks in areas that were either exposed or not exposed to shellfishing activities, we evaluated the null hypothesis that mechanical shellfishing activities leave intertidal communities intact and that they do not decrease subsequent settlement of shellfish, especially the target species. If this could be confirmed, one might consider such a fishery ‘sustainable’ (Lélé & Norgaard 1996). Unlike most studies of fishing impact (Collie et al. 2000), we monitored long-term patterns of recovery rather than quantifying direct impacts.

Materials and Methods

Main Study Site and Fishery Activities

Griend is a small uninhabited island in the western part of the Dutch Wadden Sea (53°14′N, 05°15′E; Fig. 1). The intertidal flats covered by our benthic surveys amount to about 50 km². They are exposed for 2–7 h per low-water period. Heights, and corresponding emergence times, are greatest to the east and north-east of the island. West and north-west, and south and south-west, of the island of Griend there were large mussel beds that must have been present at least since the early 1960s (Veen & van de Kam 1988). Also in the southeast, again at the boundary of the intertidal flat and the main tidal channel south of Griend, mussel banks occurred historically. From 1941, the western edge of the island of Griend has repeatedly been reshaped by various types of breakers and dikes. The last reconstructions were carried out during the summers of 1985 and 1988. A 2.5-km long sand dike was built west and north of the old circular island (Janssen et al. 1994). The central saltmarsh and creek were undisturbed.

During 26 and 27 September 1988 (full moon spring tides, westerly gale of 7–8 Beaufort, causing high water levels), six suction-dredging cockle-fishing ships worked over the intertidal flats north of the island. No cockle-ships were seen fishing on 28 September, but during the following weeks, in situations with lower tides, cockle-fishing ships were observed north-east of the island. These ships are about 10 m wide and 40 m long, with a draft of 45–50 cm. They can fish with speeds of up to 8 km h⁻¹ (Dijkema 1997), towning either one or two suction-dredges with a width from 50 cm to 115 cm. The upper layer of the sediment is first loosened by strong spouts in front of the suction-dredge. The loose upper layer is then sliced off at 2–3 cm according to the fishing companies. As this would not enable buried cockles with a diameter of 2–3 cm to be picked up, we regard 5 cm as a better estimate. The sliced material that does not ‘escape’ through a 15-mm bar mesh cage is sucked up and washed onboard over a sieve with a 15-mm mesh. The mussel beds near Griend were either dredged away or carried by hand.

By early October 1988 the sediments had been intensively reworked over a large area, with intact
Macoma shells and shell fragments lying on the sediment surface. We estimated the extent of the cockle fishery based on these surface signs, further checked by deep cores to establish that sediment reworking took place (Fig. 1). During the following 9 years, cockle-fishing ships were not observed in the study area, but limited mechanical shellfishing took place along the eastern edge of the study area late in 1995 (J.D. Holstein, personal communication).

The mussel beds near Griend remained intact in late September 1988. During the following 2 years these beds disappeared but the precise timing is unknown. No mussel banks remained when we started fieldwork in late July 1991. As elsewhere in the Wadden Sea (Beukema 1993; Beukema & Cadée 1996; Beukema, Cadée & Dekker 1998; Smit et al. 1998), the beds had been fished out, mechanically or manually, when mussel stocks were exceptionally low after a succession of years with little recruitment. We did not see mussels near Griend until August 1994 when, on intertidal flats along the main channel south of the island, two 2-ha patches of summer-settled mussel spat were found. These small beds were affected by mechanical fisheries in the course of the autumn and had disappeared by the time we returned to Griend in early August 1995. The intertidal area around Griend was divided into three areas on the basis of presence or absence and type of fishing activity. The western area had mussel beds that disappeared in 1989–91, the northern area was almost completely dredged for cockles in 1988 and the eastern area remained largely untouched and served as a reference (Fig. 1). Although the experimental and control sites were not chosen randomly, this study reflects the spatial scale of real fishing events (Hall 1999).

**SEDIMENT ANALYSES**

In early September 1988, i.e. before the cockle fishery took place, we took core samples for benthos and sediment at 500-m intervals along transects around Griend (triangles in Fig. 1). In 1992 the same samples were taken, but in later years the survey was considerably extended (Piersma & Koolhaas 1997). At each location a sediment sample was taken with a 5-cm diameter core to a depth of 7–8 cm, and stored in a closed plastic bag at room temperature for 1–4 weeks, before freezing at –30 °C. Then the entire sample was first washed in fresh water, shaking the water–sediment mix, and sieved over a 50-μm mesh. The residue that passed through the 50-μm mesh was collected and analysed to calculate median grain size. The fractions smaller than 50 μm and larger than 1000 μm (= 1 mm) were not used to calculate median grain size. The smallest fraction was analysed separately. Their removal hardly affected median grain size values. Median grain size was computed following Krumbein & Sloss (1963).
Effects of suction-dredging on bivalves

All bivalve data were collected from late July to late September, and mostly in August. Earlier, we found no seasonal effects on abundance or biomass of bivalves over the period July–October (Piersma et al. 1993). Up to 1992 benthic abundances were monitored along a series of transects radiating from the island, starting 100 m offshore from the high-tide mark (triangles in Fig. 1). Along the transects cores were taken and sieved at 500-m intervals. In 1993 this system was replaced by a mapping method using a fixed grid at 250-m intervals, with sampling points at each grid intersection (dots in Fig. 1).

The bivalves in the western and northern areas at Griend were mapped in August–September 1988, just before the cockle-fishing in late September. After the cockle-dredging, due to the reworking of the sediments that led to the presence of large quantities of dead shells in the upper layer, sampling became difficult and sometimes impossible. Even in 1989 sieving and sorting the sediments at the fished transects was so difficult that we decided not to sample them that year.

Sampling locations along transects were found by pacing out the distance with a calibrated step-length and a hand-counter, using a compass to walk in the appropriate direction. Locations away from the transects were found by cross-reading the compass bearings on conspicuous landmarks. From 1993 the predetermined positions were found with a Philips AP-navigator (Philips, Eindhoven, the Netherlands), using the Europe-wide DECCA radio-beacon system (defunct since the mid-1990s), or using a hand-held Global Positioning System (GPS) (Garmin 45, Garmin Corporation, Lenexa, KS). To sample the bivalves, at each sampling station we took 20 sediment cores of 1/56 m² down to a depth of 20 cm and sieved each of them over a 1-mm mesh. The residue of each core was put into a separate identifiable plastic bag and stored frozen until laboratory treatment. In the more recent grid-mapping approach only one sediment core of 1/56 m² was taken at each point, but sampling depth did not change.

To compare the results of the benthic transects and the grid mapping, both methods were applied simultaneously in August 1993 (Piersma & Koolhaas 1997). For both Cerastoderma and Macoma, small individuals were better represented in the transect than the grid because samples on transects were numerically biased toward high flats where most settlement occurs. For Macoma the grid method yielded lower abundance and higher biomass values than transects. These contrasting effects were small and we refrained from adjusting the abundance measures for Macoma. As we sampled no deeper than 20 cm, only data for Mya smaller than 40 mm are presented, larger ones of this species living deeper in the sediment (Zwarts & Wanink 1984).

In the laboratory, the molluscs in each bag were counted and their maximum length measured to the nearest millimetre. In the case of bivalves, the flesh was removed from the shell and dried to constant mass at 55–60 °C and incinerated at 550 °C for 2 h to obtain species-, length-, site- and year-specific values of ash-free dry mass (AFDM) (Piersma et al. 1993). These data served as the basis for all abundance and biomass values presented here.

Settlement of bivalve spat at sites other than Griend

The settlement of small bivalves after their pelagic larval phase (spatfall) is widely studied (Beukema, de Bruin & Jansen 1978; Beukema 1989, 1992; Beukema et al. 1993). To evaluate the effect of cockle-dredging on juvenile bivalves we assembled data on post-settlement densities of Cerastoderma and Macoma for five different sites from much of the Dutch Wadden Sea. None of the non-impacted reference sites were all in the west of the Dutch Wadden Sea and the treatment sites more spread out (cf. Fig. 8a), we would expect this to affect the analyses only if they showed congruent patterns in the degree of shelter from storms and wave action. In both the treatment and the reference group, two types of sites with respect to shelter were included. Some sites (Hengst and Balgzand) had little shelter from nearby dikes, islands or extensive intertidal areas and were thus exposed to winter storms and wave action, and some (Balgzand, Piet Scheve Plaat and Groningen) were relatively sheltered.

Bivalve abundances at the sites Piet Scheve Plaat and Groningen were obtained from a Rijkswaterstaat monitoring programme. For Groningen, data were used from location 54–1 (Essink 1978). At this location, each year in August–September 20 cores of 1/131 m² each were taken to a depth of 30 cm. At Piet Scheve Plaat core samples were taken along three transects. At each 760-m long transect 20 equidistant cores of 1/116 m² were taken (Dekker 1997). Samples were sieved in the field over a 1-mm mesh. The bivalves in the fraction that remained on the sieve were counted and measured soon afterwards in the laboratory. Although cockles were fished in the vicinity of the sampling location Groningen (between 1 and 15 September 1993, and in late August 1995), the site itself was not touched. In 1996–98 no cockles were fished at all in the vicinity of the Piet Scheve Plaat and was dredged for cockles in the 1980s up to 1998 (see Fig. 8a). Two of the sites (Griend and Balgzand) contained an area that had been affected by cockle-dredging in the late 1980s in addition to a non-impacted reference area. Another site (Hengst) had not experienced cockle-dredging in the late 1980s, and two sites (Piet Scheve Plaat and Groningen) were dredged for cockles in the late 1980s. Although the non-impacted reference sites were all in the west of the Dutch Wadden Sea and the treatment sites more spread out (cf. Fig. 8a), we would expect this to affect the analyses only if they showed congruent patterns in the degree of shelter from storms and wave action. In both the treatment and the reference group, two types of sites with respect to shelter were included. Some sites (Hengst and Balgzand) had little shelter from nearby dikes, islands or extensive intertidal areas and were thus exposed to winter storms and wave action, and some (Balgzand, Piet Scheve Plaat and Groningen) were relatively sheltered.

At Hengst, sediment cores of 1/56 m² were taken at a variable number of locations evenly spaced according to a 250-m grid. Cores had a depth of 20 cm and were sieved over a 1-mm mesh. Samples were processed as...
described for Griend. The number of sampling stations used varied from 21 in 1992 to 100 in 1998. At Balgzand, annually in August starting from 1973, 20-cm deep samples were taken at 15 stations (12 transects of 1 km length and three squares of 900 m$^2$) covering a total of about 0.45 m$^2$ per station (for details see Beukema 1974). Three of these stations were mechanically fished in autumn 1988 or in 1990, and served as a comparison for the 10 stations that were not subjected to shellfishing activities. Two low-lying stations were only rarely settled and were left out of the comparison. Data from the entire Balgzand area were also used to assess whether standing stocks of Cerastoderma and Macoma were uniquely high in 1988, just before the fishery.

**Experimental design and statistics**

To test for the effects on sediment characteristics (median grain size and silt content) of area and fishing treatment, time (year, or combination of years) and the interactions between area and time, simple analyses of variance were applied, using individual sediment samples as replicates. The eastern segment of the flats served as the control for the two areas that were affected by either cockle-dredging or the removal of two mussel bed complexes (Fig. 1).

The geographical and temporal spread of the fishing effort around Griend allowed us to analyse statistically the effects on bivalve abundance as a single large-scale and long-term experiment according to a 'before/after and control/impact' (BACI) design (Schmitt & Osenberg 1996). More specifically, the BACI-variance of paired series (BACIPS) was used (Stewart-Oaten, Murdoch & Parker 1986; Schmitt & Osenberg 1996).

As the experiment was unplanned, the abundance measures of bivalves in the 'before' situation were determined only once (in 1988). As outlined below, during 1990–95 the sediments of the cockle-dredged area were relatively coarse but fairly stable before returning (in 1996–98) to a state that resembled the initial situation. We thus had six annual average values from the period 1990–95 as replicates for the 'after' situation to compare with the single value from 'before'. There was no evidence of temporal autocorrelation in the measures of abundance during this period. As expected, only one of the 27 correlation coefficients was significantly different from zero under $P < 0.05$.

To ensure normality of the data on bivalve abundance, average numerical and biomass densities were log-transformed. We then calculated the differences in the log-transformed abundance measures for Cerastoderma, Macoma and Mya between reference and experimental areas. These differences equalled the log-transformed ratios of the untransformed abundance measures. Based on the six 'after' observations for the period 1990–95, the 95% prediction intervals for the log-transformed ratios were calculated based on the $t$-test (Sokal & Rohlf 1981). To test whether $H_0: \mu_1 = \mu_2$ can be falsified, it has to be determined whether the single 'before' observation falls in this predicted interval. If it does, there has been no significant change with respect to the difference between areas (i.e. $H_0$ is not rejected; there is no effect of treatment). If the single 'before' observation falls outside the predicted interval, it can be concluded that the specific treatment does have a significant effect on the abundance measure (with $P < 0.05$). The most insightful comparison was between the reference area and the area dredged for cockles, but we also compared the differences between the reference area and the area from where mussel beds were removed, as well as the differences between the two fished areas.

Although the design ensured that temporal fluctuations at the reference and experimental areas did not confound the detection of the fishery impact, any location-specific temporal difference would be interpreted as an impact (Underwood 1992, 1996). With regard to patterns in settlement of bivalves we extended the analysis beyond BACI by also using data from locations other than Griend. It turned out that in 1995 one area (Hengst) was not well covered. We therefore averaged the spatial means for a late period (1992–94) and a late period (1996–98) and calculated the ratio of the two for each (sub)location. Log-transformed ratios are normally distributed and differences between fished and unlished areas were tested for significance by Student's $t$-tests. All statistical analyses were carried out in SYSTAT.

**Results**

**Sediment characteristics around Griend**

The first comprehensive assessment of sedimentary characteristics after the cockle-dredging in 1988 took place in 1992 (Fig. 2). Over all three areas, average median grain size increased from 166.2 µm (SD = 14.0, $n = 16$) to 174.2 µm (SD = 14.1, $n = 30$), with a further increase to 179.1 µm (SD = 16.3, $n = 28$) in 1994. A two-way analysis of variance showed that the difference between 1988 and 1992 was significant ($F_{1,39} = \text{6.614, } P = 0.012$) and an effect of area ($F_{2,40} = \text{15.184, } P = 0.002$). There was also an important effect of area ($F_{2,39} = \text{12.071, } P = 0.0001$) but no significant interaction between the two factors ($F_{2,39} = \text{1.482, } P = 0.239$). This indicated that, although there were differences in median grain sizes between areas, there were no differences among areas in the changes in median grain size between 1988 and 1992.

Between 1994 and 1998 there was a decline in median grain size in the area previously dredged for cockles (Fig. 2), and values seemed to return to the prefisheries level. A two-way analysis of variance indeed showed a significant difference between 1994 and 1998 ($F_{1,39} = \text{7.010, } P = 0.012$) and an effect of area ($F_{2,39} = \text{7.138, } P = 0.002$), but again no significant interaction between the two factors ($F_{2,39} = \text{1.784, } P = 0.181$). A two-way
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analysis of variance, assuming that sediment samples collected in the periods 1992–94 and 1996–98 yield two sets of independent data points, confirmed a significant difference between the first and second period ($F_{1,153} = 5.687$, $P = 0.018$), a large effect of area ($F_{2,153} = 22.456$, $P < 0.0001$), and a significant interaction term between the time and place ($F_{2,153} = 4.499$, $P = 0.013$).

A similar analysis was carried out for silt content (Fig. 3), a sediment characteristic that tends to be much more variable as a consequence of surface perturbations (van Straaten 1965). A two-way analysis of variance for the differences between 1988 and 1992 showed a strong effect of area ($F_{2,40} = 10.31$, $P < 0.0001$) but no effect of year ($F_{1,40} = 1.233$, $P = 0.273$), nor of interactions between area and year ($F_{2,40} = 0.009$, $P = 0.991$). A comparison between 1988 and 1994 did not show significant effects or interaction terms either. The low silt content in 1988–94 was followed by a steep increase up to 1998, especially in the area previously dredged for cockles (Fig. 3). A comparison between 1994 and 1998 indeed showed a significant effect of year ($F_{1,38} = 10.556$, $P = 0.002$), no effect of area ($F_{2,38} = 2.168$, $P = 0.128$) and a significant interaction term between area and year ($F_{2,38} = 4.957$, $P = 0.012$). So the increase in silt content after 1994 was significant, and so were differences in the extent of the increase between areas.

In summary, there were significant temporal changes in the two sediment characteristics over the period 1988–98, and in several cases the magnitude of these changes differed significantly between the three areas around Griend. The sedimentary changes were most pronounced in the area dredged for cockles (Figs 2 and 3), with an increase in median grain size and a reduction in silt content from 1988 to 1994 being followed by a return to pre-impact conditions 8–11 years after the fishery.
The dredging of cockles in September and October 1988 took place in an area where cockle biomass and total density were higher than in the other two areas (Fig. 4 and Table 1). The limited extent of mechanical cockle-dredging carried out along the eastern edge of the reference area in 1995 was reflected by the low biomass of *Cerastoderma* in 1996. In the area dredged for cockles in 1988, peaks in settlement occurred in 1991 and 1996, whereas in the reference area settlement showed peaks of increasing height in 1990, 1992, 1994 and 1997 (Fig. 4). There was a significant treatment effect on the differences in abundance of *Cerastoderma* between the reference area and the area dredged for cockles (Table 1). Whereas biomass and total density were lowest in the reference area before the fishery incident, these abundance measures were significantly higher afterwards (Table 1). The same difference occurred between the reference and the mussel area, indicating that the mechanical cockle harvest negatively affected the standing stocks of *Macoma*. Nevertheless, a reverse pattern was shown by total and spatfall density of *Macoma* (Table 1; note that, particularly in this species, total densities are almost entirely comprised of spatfall). This indicated that spatfall densities in the reference and mussel areas, relative to the cockle area, decreased after the fishery events.

**Fig. 4.** Changes in biomass (left panels), numerical density (middle panels) and the density of spatfall (right panels) of edible cockles *Cerastoderma edule* in the three experimental areas around Griend from 1988 to 1998. The error bars indicate 1 SE.

Biomass of *Macoma* was higher in the area dredged for cockles than in the reference and mussel areas before the fisheries in 1988 (Fig. 5 and Table 1). As with *Cerastoderma*, before the cockle fishery the biomass of *Macoma* was lowest in the reference area compared with the area dredged for cockles but significantly higher afterwards (Table 1). The same differences were found between the reference and the mussel area, and between the mussel and cockle area, indicating that the mechanical cockle harvest negatively affected the standing stocks of *Macoma*. Nevertheless, a reverse pattern was shown by total and spatfall density of *Macoma* (Table 1; note that, particularly in this species, total densities are almost entirely comprised of spatfall). This indicated that spatfall densities in the reference and mussel areas, relative to the cockle area, decreased after the fishery events.

Soft-shelled clams *Mya* < 40 mm in length were rarely encountered on the intertidal flats around Griend until there was strong recruitment, especially in the reference area, in 1991, 1994 and 1996 (Fig. 6). For *Mya*, differences in density between the reference area on the one hand and the cockle and mussel areas on the other became significantly larger after the fishery events (Table 1).

Thus, on the basis of either the biomass or the density measures, for all three species there was evidence...
Table 1. Multiple comparisons of the abundance measures for the three bivalve species Cerastoderma, Macoma and Mya between different ‘treatments/areas’ at Griend (Figs 4–6) relative to the occurrence of fishery activities (Before = 1988 and After = 1990–95). ‘Cockle’ is a shorthand for ‘area dredged for cockles’ and ‘mussel’ means ‘area where mussel beds were removed’ (Fig. 1). The factorial difference in abundance between two treatments T1 and T2 is indicated by the T1/T2 ratios presented (these were all back-transformed from the logarithms used in calculations). A statistically significant difference (P < 0.05) between the ratio before (RB) and the ratio after the fishery activities (RA) (i.e. if R_B > R_A) indicates in the last column by R_B < R_A), means that the difference in abundance between the treatment areas has changed. If R_B > R_A then the abundance in T1 compared with T2 has significantly increased. If R_B < R_A, then the abundance in T1, compared with T2, has increased.

<table>
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<th>Comparison (T1 vs. T2)</th>
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<td>4.47</td>
<td>R_B &gt; R_A</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Macoma</td>
<td>Spatfall</td>
<td>Density</td>
<td>5.47</td>
<td>3.06–9.79</td>
<td>54.27</td>
<td>R_B &gt; R_A</td>
<td></td>
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<tr>
<td></td>
<td>Mya</td>
<td>All ages</td>
<td>Biomass</td>
<td>0.50</td>
<td>0.00–46.95</td>
<td>1.00</td>
<td>NS</td>
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<tr>
<td></td>
<td>Mya</td>
<td>All ages</td>
<td>Density</td>
<td>2.75</td>
<td>2.17–3.48</td>
<td>1.00</td>
<td>R_B &lt; R_A</td>
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<td></td>
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<td>Spatfall</td>
<td>Density</td>
<td>3.99</td>
<td>0.40–39.37</td>
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<td>NS</td>
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<td>Reference vs. mussel</td>
<td>Cerastoderma</td>
<td>All ages</td>
<td>Biomass</td>
<td>2.98</td>
<td>1.11–8.02</td>
<td>0.51</td>
<td>R_B &lt; R_A</td>
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<tr>
<td></td>
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<td>All ages</td>
<td>Density</td>
<td>3.21</td>
<td>2.85–3.63</td>
<td>1.63</td>
<td>R_B &lt; R_A</td>
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<tr>
<td></td>
<td>Cerastoderma</td>
<td>Spatfall</td>
<td>Density</td>
<td>2.65</td>
<td>1.76–3.99</td>
<td>2.33</td>
<td>NS</td>
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<tr>
<td></td>
<td>Macoma</td>
<td>All ages</td>
<td>Biomass</td>
<td>1.61</td>
<td>1.45–1.80</td>
<td>1.19</td>
<td>R_B &lt; R_A</td>
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<tr>
<td></td>
<td>Macoma</td>
<td>All ages</td>
<td>Density</td>
<td>3.75</td>
<td>3.47–4.05</td>
<td>4.25</td>
<td>R_B &gt; R_A</td>
<td></td>
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<tr>
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<td>Macoma</td>
<td>Spatfall</td>
<td>Density</td>
<td>7.24</td>
<td>6.54–8.02</td>
<td>7.91</td>
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<td>Mussel vs. cockle</td>
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<td>0.45</td>
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<td>0.42–1.31</td>
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<td></td>
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<td>Spatfall</td>
<td>Density</td>
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<td>5.98</td>
<td>R_B &gt; R_A</td>
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<td>Macoma</td>
<td>All ages</td>
<td>Biomass</td>
<td>0.84</td>
<td>0.67–1.05</td>
<td>0.55</td>
<td>R_B &lt; R_A</td>
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<tr>
<td></td>
<td>Macoma</td>
<td>All ages</td>
<td>Density</td>
<td>0.74</td>
<td>0.64–0.85</td>
<td>1.05</td>
<td>R_B &gt; R_A</td>
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<tr>
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<td>Spatfall</td>
<td>Density</td>
<td>0.76</td>
<td>0.44–1.28</td>
<td>6.86</td>
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<td>All ages</td>
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<td>Spatfall</td>
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<td>1.39</td>
<td>0.05–42.16</td>
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for statistically significant negative effects of shellfishing (especially cockle-dredging) on overall bivalve abundance (Table 1). Perhaps surprisingly, in none of the three bivalve species was there statistical evidence that juvenile settlement was reduced as a consequence of the fishery (significant positive trends even occurring in Cerastoderma and Macoma). These slightly confusing results could have resulted from competitive adult–juvenile interactions (Hancock 1973; Beukema 1982; Olafsson, Peterson & Ambrose 1994) contributing to the particularly low spatfall densities in the highly cockle-rich dredged area in 1988. Nevertheless, especially in the area dredged for cockles (Figs 4–6), densities of spatfall of all three species were noticeably higher in 1996–98 (years with small median grain sizes, high silt content) compared with 1990–95 (years when sediments were relatively coarse). The increase equalled a factor of 1.8 in Cerastoderma, 3.8 in Macoma and 2.3 in Mya. That none of the differences based on log-transformed annual averages reached significance (Student’s t-tests, P > 0.1) was not surprising given the short period (3 years) over which the reversed sediment characteristics occurred and the response of the settling bivalves could be studied.

WERE BIVALVE STOCKS EXCEPTIONALLY HIGH IN 1988?

During the first 6 years after the fishing in 1988, median grain sizes were high (Fig. 2), silt content was low (Fig. 3) and spatfall densities of bivalves were also quite low (Figs 4–6). Probably as a consequence, the overall biomass of Cerastoderma failed to recover from the fishing in late 1988 and there was a steady decline in overall standing stock of Macoma (Fig. 7; for biomass on year the Spearman rank correlation coefficient z = –0.905, P < 0.05). One could argue that these patterns were entirely due to Cerastoderma and Macoma stocks having reached uniquely high levels in the year 1988. No long-term data are available for the intertidal flats around Griend to examine this possibility, but such data do exist for Balgzand, c. 60 km to the south-west in the Wadden Sea. Such a comparison is valid not only because of the proximity of the two intertidal flat systems, but also because changes in macrobenthic abundance tend to be synchronized over large parts of the Wadden Sea (Beukema et al. 1993; Beukema, Essink & Michaelis 1996).

Cerastoderma stocks at Balgzand were high in 1988, as they were around Griend, but even higher stocks...
Fig. 5. Changes in biomass (left panels), numerical density (middle panels) and the density of spatfall (right panels) of Baltic tellins *Macoma balthica* in the three experimental areas around Griend from 1988 to 1998. The error bars indicate 1 SE.

Fig. 6. Changes in biomass (left panels), numerical density (middle panels) and the density of spatfall (right panels) of soft-shelled clams *Mya arenaria* in the three experimental areas around Griend from 1988 to 1998. The error bars indicate 1 SE.
Effects of suction-dredging on bivalves

were found in 1980, 1981, 1991 and 1994 (Fig. 7, top). In view of the published evidence for macrobenthic synchronization in the Wadden Sea, cockle stocks at Griend in 1988 were unlikely to be exceptional. For *Macoma* the picture for Balgzand told an even clearer story (Fig. 7, bottom). Between 1978 and 1998 there were 7 years when stocks exceeded those of 1988 and 9 years when stocks were smaller.

The evidence presented so far demonstrates significant negative effects of mechanical shellfishing on overall bivalve abundance, but is less clear about the role of recruitment in causing the strong relative decline of bivalves in the dredged area. The BACIPS comparisons (Table 1) provided no evidence for negative effects of mechanical shellfishing on bivalve settlement within the first 8 years after fishing (in fact, sometimes the contrary). However, the strong recruitment of *Cerastoderma* and *Macoma* in the subsequent 3 years, especially in the dredged area where sediment characteristics returned to initial values, suggested that dredging may indirectly affect bivalve recruitment through its impact on the sedimentary environment. It was possible to examine further the effect of this fishery on bivalve settlement using the log-transformed ratios of spatfall densities for an early period (1992–94) and a late period (1996–98) for five areas that did or did not experience cockle-dredging in the 1988–90 period (Fig. 8a).

For *Cerastoderma* (Fig. 8b), the difference in log-ratios of fished and unfished areas was highly significant (separate-variance model, $t = 5.720$, d.f. = 4.4, $P = 0.003$). The initial failure of *Cerastoderma* stocks to recover in the area dredged for cockles near Griend may thus have been a consequence of reduced recruitment and not due to some odd local phenomenon other than mechanical fisheries. The long-term absence of high cockle densities appeared to be a genuine effect of the mechanical cockle fishery.

For the non-target species *Macoma* (Fig. 8c), a difference in settlement between fished and unfished areas could not be confirmed statistically. The direction of the difference was the same as for *Cerastoderma*, but the power of our test was not large enough to show that the ratios for fished areas were significantly lower than ratios for unfished areas ($t = 2.053$, d.f. = 3.7, $P = 0.116$).

**Discussion**

**SPATIAL SCALES AND THE LIKELIHOOD OF DETECTING EFFECTS**

The strengths of this study are, first, its spatial scale, comparing adjacent treatment and reference areas of 10–15 km$^2$ and also comparing sampling areas of varying in size from less than 1 km$^2$ to 15 km$^2$ that are up to 100 km apart. Secondly, we followed the recovery process over 10 years. Its weaknesses are inevitably the lack of treatment replication for the Griend example, in the limited run of pretreatment data, and in the non-random allocation of treatment or reference areas in the overall Wadden Sea comparison. The value of the comparison between the cockle-dredged and reference area near Griend may have been limited by the fact that the reference area consisted of relatively high and sheltered intertidal flats, whereas most of the dredged area was lower and more exposed to storms and wave action. Nevertheless, the comparisons involve realistic manipulations and the problems are partly compensated by the internally time-paired comparisons between treatment and reference (Stewart-Oaten, Murdoch & Parker 1986). In addition, the contrasts that we found in the long term trends in recruitment of *Cerastoderma* and *Macoma* were confirmed for similarly contrasting recruitment patterns at sites far away from the core study area near Griend (Fig. 8).
Variations in local geomorphology are therefore unlikely to have biased the conclusions with respect to the long-term effects of cockle-dredging.

On the basis of experiments to study the effects of cockle-dredging on non-target species in an intertidal area in Scotland, Hall & Harding (1997) concluded that, although the non-target benthic fauna may suffer high levels of mortality, ‘recovery is rapid and the overall effect on populations is probably low’ (but see Ferns, Rostron & Siman 2000). Hall & Harding (1997) also suggest that effects might vary with plot size. Their experimental plots varied in size between 0·02 ha (the smallest tractor-dredged surfaces) and a maximum of 0·5 ha (suction-dredged plots), with the total fished area covering 7 ha out of a total of over 100 ha (Hall & Harding 1997, fig. 3). This may explain why our conclusion differs from theirs: mechanical cockle-dredging at the scale at which it normally takes place, in our case covering about 1500 ha of a total of 5000 ha of intertidal flats (Fig. 1), appears from our data to have considerable effects on the target and non-target species. Also, their study took place in an area that had been exposed to fishing and may have adjusted to such disturbances (Roberts 1997; Norris, Bannister & Walker 1998; Hall 1999). As is clear from a recent meta-analysis of fishing impacts on benthic communities (Collie et al. 2000), the disturbance caused by cockle-dredging needs qualification.

**SEDIMENT CHARACTERISTICS AND THE SETTLEMENT OF BIVALVES**

Reduced settlement explained the 8-year long decline in shellfish stocks around Griend after 1988. Dredging, especially in stormy conditions, causes the loss of fine silts (Churchill 1989; Hall 1994), which may explain why the sediments became somewhat coarser in the dredged area and attracted smaller densities of bivalve spat than after the reversal to initial conditions (Batham 1987, Thrush et al. 1996, 1997). We did not find clear differences in sediment characteristics between the reference area and the area where the mussel beds disappeared, but the loss of habitat complexity and sediment trapping by the nearby mussel beds may have aggravated the effects of cockle-dredging (Oost 1995; Meadows et al. 1998). The loss of adult shellfish stocks may have had the added effect that faeces and pseudo-faeces were no longer produced, the lack of which could also have contributed to the loss of silt (Verwey 1952; Hertweck & Liebezeit 1996).
Effects of suction-dredging on bivalves

Especially in unconsolidated sediments, physical disturbances from natural (storms) and unnatural causes (dredging) can greatly affect the benthic fauna (Hall 1994; Wildish & Kristmanson 1997; Newell, Seiderer & Hitchcock 1998). As benthic organisms can substantially alter the properties of sediments by influencing interparticle adhesion, grain size distribution through the formation of faecal pellets (biodeposition), sorting of grain sizes, water content and the formation of structures, all of which relate to the stability of the sediments, the latter type of communities have low secondary productivity (Emerson 1989); much primary productivity remains unused by the benthic consumers (Beukema & Cadée 1997; Newell, Seiderer & Hitchcock 1998; Hall 1999). Due to the many stress factors, the latter type of communities have low secondary productivity (Emerson 1989); much primary productivity remains unused by the benthic consumers (Beukema & Cadée 1997; Newell, Seiderer & Hitchcock 1998; Hall 1999). According to this hypothesis, the mechanical removal of the large filter-feeding bivalves initiates sedimentary changes that lead to the disappearance of other filter-feeders such as Macoma. At that point these filter-feeders can no longer produce the faecal pellets that play such an important role in the build-up of fine-grained sediments (Risk & Moffat 1977) that, in turn, attract settling bivalve larvae. The strength of such a negative feedback loop can be increased by winter storms that churn up the upper layer of sediments.

The intertidal flats examined in this study showed recovery with respect to spattfall of Cerastoderma and Macoma within a period of 10 years, perhaps reflecting a change from one ‘stable’ state to another (van de Koppel et al. 2001). The reversal of sedimentary characteristics occurred between 1994 and 1996. The winter of 1995–96 was cold, and calm in terms of wind conditions (data of Royal Dutch Meteorological Service, KNMI, De Bilt, the Netherlands). Therefore, the absence of major storms may have triggered this reversal. If this was true, not only would the recovery of mechanically fished areas greatly depend on chance conditions such as the incidence of winter storms, but repeated mechanical shellfisheries (especially in combination with stormy winters) could well compromise this reversibility.

We believe that the large intertidal flat system south of Richel and Vlieland (Waardgronden) provides a case in point. Historically, these flats were quite muddy (Postma 1957) and rich in cockle and mussel beds (Kruger 1939, 1940; Kristensen 1957). Now the beds are no longer present and the flats have turned into a large expanse of sandy flats low in silt where bivalves are few (Postma 1957). Historically, these flats were quite muddy (Postma 1957) and rich in cockle and mussel beds (Kruger 1939, 1940; Kristensen 1957). Now the beds are no longer present and the flats have turned into a large expanse of sandy flats low in silt where bivalves are few (Postma 1957).

Conclusions

After extensive experimentation on a New Zealand sandflat, Thrush et al. (1996) concluded that large-scale disturbances that destroy organisms with a role in maintaining habitat stability, such as the mussel and cockle beds in the Wadden Sea, are likely to result in very slow recovery dynamics, particularly in wave-disturbed soft-sediment habitats. In line with this, we propose that cockle-dredging of large areas of intertidal flat in the Dutch Wadden Sea in the late 1980s, perhaps in combination with the destruction of nearby all intertidal mussel beds, temporarily transformed relatively untrysted mid-shore communities living under relatively mild abiotic conditions into benthic communities typical of mobile sands low in silt and organic matter (Beukema & Cadée 1997; Newell, Seiderer & Hitchcock 1998; Hall 1999). Due to the many stress factors, the latter type of communities have low secondary productivity (Emerson 1989); much primary productivity remains unused by the benthic consumers (Beukema & Cadée 1997). Impact studies commissioned by the Dutch government (de Vlas 1982, 1987a,b) and reviews commissioned by the shellfishing industry (de Haan 1991) concluded that the ecological effects of suction-dredging are minor and of short-term duration. Our conclusion, that cockle-dredging leads to a significant long-term reduction in settlement and stocks of the target species, is therefore at variance with advice previously given to the Dutch government.

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